# A variable edge effect on trees of Bwindi Impenetrable National Park, Uganda, and its bearing on measurement parameters

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## ARTICLE INFO

## ABSTRACT

With tropical forests under increased pressure from fragmentation and nascent effects of climate change, it is imperative to reliably predict change for timely reduction of impacts. This depends on measuring the right variables and analyzing them in ways that best detect change. I compared the usefulness of density, species richness, species diversity, and size in detecting edge penetration; and other parameters in revealing edge effect on tree species in Bwindi Impenetrable National Park, Uganda. Trees were sampled in 104 1 km edge-interior transects set around the entire park. Density and species richness were better indicators of edge-width than girth size and diversity measurements, both showing edge penetration as most intense within 300 m, although effect was detectable up to 900–1000 m. This estimate compared closely with an earlier estimate of 300–350 m obtained using incidences of resource harvest. Among other measures, measures of tree species abundance and frequency showed significant response to the edge by both early succession and primary forest species; while analyses of density showed edge response primarily by forest interior species. Parameters of tree size and their derivatives showed edge response by the lowest number of species. These results suggest that to measure edge effects reliably, it is important to select the right parameters.

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## 1. Introduction

Edge effects, the diverse environmental changes associated with abrupt artificial boundaries of forest fragments are important determinants of species persistence in habitat islands (Laurance et al., 2006; Newmark, 2008). For example, human-related edge effects like wildlife snaring, poisoning, and disease (Newmark, 2008) have been identified as important determinants of large carnivore persistence in east African reserves (Woodroofe and Ginsberg, 1998), and abrupt shifts in floristic composition have been shown to be accelerated by mortality and recruitment of trees within ≈100 m of fragment margins in the Amazon resulting in plant population declines and extinctions (Laurance et al., 2006).

For plant species, individual responses to edges are in part determined by physiological tolerances (Tilman and Downing, 1994; Colinvaux, 2005; Laurance et al., 2006) and studying these responses has been the aim of many studies of edge effects on vegetation. As such, it is now well known that vegetation patterns vary in relation to forest margins (e.g. Laurance and Bierregaard, 1997; Laurance et al., 2007). Opening up new edges exposes organisms to increased risk of des-

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iccation as edges tend to be drier, have increased exposure to light, and are strongly disturbed by wind, conditions otherwise buffered in absence of edges (Murcia, 1995). Soil nutrient levels and regimes may also be altered near edges (Edmonds and Bigger, 1984; Forman, 1986). Forest edge plants may also be stressed by anthropogenic influence, particularly through resource harvest, fire burns, livestock grazing, invasion of exotic species, and vegetation clearing (Olupot, 2006; Olupot et. al., in review-a). Other effects may be cascading multipliers arising from changes in climatic or anthropogenic pressure (Laurance, 1998) and resulting from altered intensities and directions of competitive, predatory, parasitic, symbiotic, and other interactions which determine the survival and reproduction of individual species.

In addition to understanding edge effect on individual species, studies of edge effects are also in part driven by the need to determine the degree to which habitats have been altered by influence of edges. The ratio of habitat edge to the interior is the parameter of interest in this case. As traditional stressors of natural ecosystems can be exacerbated by climate change (CCSP, 2008), effects of edges can be similarly expected to increase, further reducing the quality of habitat islands. As they are a dynamic front in which habitat change can be observed, edge ecotones and elevation gradients are thought to offer an important opportunity for detecting the effects of climate change on tropical forest plants. They are therefore recommended as potential sites for monitoring (Clarke, 2007).

So far, studies of edges can be separated into those describing species abundance and richness near edge habitats without evaluating underlying causes for those distributions, and those that attempt to discover alteration in processes (e.g. predation, parasitism, seed germination, seedling recruitment, fruit production, mortality, nutrient cycling, wind action) affecting species distributions and abundance near edges (Kremsater and Bunnel, 1999). Presently, no studies have expressly discussed the power of different approaches in analyzing edge effects. In a review of tropical forest responses to global environmental change, Clark (2007) noted that while progress has been made in recent years on standardizing and refining research approaches, a number of methods and data-limitations continue to affect efforts both to detect within-forest changes and to relate them to ongoing environmental change. Among other concerns, the author noted the need for improved sampling designs, longer time-series of observations, filling key data gaps, and data access. Needless to say, parameters used for analysis may be part of the limitations.

This paper compares results of different approaches of analyzing edge effects, with the objective of evaluating effectiveness of each in detecting edge-width, and edge response by individual species. The main question addressed therefore is: how do results change when different variables and analyses are used to measure edge effect? A secondary question was: what do these analyses say about edge-effect at the site of study?

The data used were collected from Bwindi Impenetrable National Park (BINP), Uganda. Other estimates of edge penetration in the same forest have measured anthropogenic factors and distribution of exotic plants (Olupot and Chapman, 2006; Olupot et al., in review). The potential influence of the edge

on this park is also strong, as it is an abrupt transition from forest to heavily settled and cultivated land. BINP is also interesting because of its high conservation value, being home to many globally threatened species including the mountain gorilla (*Gorilla beringei beringei*) and the common chimpanzee (*Pan troglodytes scweinfurthii*). Thus, results generated can also be used to help in the design of monitoring activities. I focus on plants because unlike fauna, relatively few studies have examined effects of edges on flora (Laurance et al., 1997).

## 2. Materials and methods

### 2.1. Field methods

Bwindi Impenetrable National Park is located 0° 53′–1° 08′S, 29° 35′–29° 50′E in southwestern Uganda. The park, 321 km² in area, lies on a rugged terrain adjacent to the Uganda/DRC border, spanning a wide altitudinal range with elevation being 1190 m and 2607 m asl at the lowest and highest points respectively (Thomas Butynski, unpublished data 1984). The area surrounding the park is densely settled, thus, an abrupt edge separates forest from surrounding farmland and settlements.

This paper is based on data collected during the period 2001–2003. Data were recorded from 104 1 km edge-interior perpendicular transects located around the park boundary. Eight transects were set equidistantly in each of the parish-park interfaces >5 km long. A parish is the smallest administrative unit in Uganda. Coordinates of transect start points were read off on paper using a map of the park and adjacent parishes overlaid with a UTM grid. Transect start points were reached in the field by locating the coordinates using handheld GPS units.

Trees were sampled in variable area plots spaced at 100 m intervals along transects, with the first plot centered on the boundary line. Compared with fixed area approaches, variable area approaches are quick and easy to apply, even in difficult terrain. Also, the amount of information collected varies little with stem densities (Sheil et al., 2002). Within each plot, 15 trees nearest to the 100 m mark were identified and measured, and distance to the furthest tree was taken as the radius of the plot. Only measurements and identities of trees with diameter at breast height (DBH) of >10 cm taken 1.3 m above ground or just above buttresses were recorded. Trees were sampled only in plots where the nearest tree was <5 m, and the furthest tree <40 m from a meter-mark. All transect lengths were corrected for slope such that transect distances of 1 km were actually horizontal distances on the ground.

### 2.2. Data analysis

Analyses were performed at two general levels; first for all species combined, and then for each species individually. I used variables commonly used in vegetation analysis. Some of the parameters used to measure edge-effect and effects of disturbance on plants are density, species richness, size, mortality, floristic composition, abundance (reviewed in Laurance and Bierregaard, 1997; Laurance et al., 2006); importance value index, relative dominance, relative frequency, relative density (e.g. Barker et al., 2002); basal area, above ground biomass, area leaf index, understory light availability,

and percent canopy openness and vegetation cover (Mayaux et al., 2005).

Community-level parameters used for determining edge-width were density, girth size, species richness, and species diversity. Function displays and between-sample comparisons of means using t-tests and standard errors were used where appropriate. Species richness was calculated as the number of species in a given sample, and species diversity was determined using Fisher's alpha diversity index (Fisher et al., 1943). Fisher's alpha ($\alpha$) was given by the equation $\alpha = (N [1-X])/X$, where X was calculated from the equation $S/N = (1-X)/X (-\ln[1-X])$ and S represented the number of species, while N represented the number of individuals per plot or plot category. Another parameter used to explore gradients at community level was change in species composition. Data were summarized by parish to fit within the spreadsheet format, and then log-transformed to permit a smooth linear or curvilinear relation between dissimilarities and distances. It was then scaled to two ordination axes using non-metric multidimensional scaling (NMDS) with Kruskal's STRESS formula 1 as the loss function. The relationship between the axes and edge-proximity was assessed using Pearson correlations.

Species-level analyses explored edge-related variation for individual species. At the outset, 11 variables were used. These were diameter at breast height (DBH), basal area, density, relative density, abundance, relative abundance, frequency, relative frequency, dominance, relative dominance, and importance value index (IVI). They were defined as follows:

- DBH = diameter at breast height (i.e. 1.3 m above ground).
- Density = number of trees/plot area.
- Relative density = density of trees of a given species/density for all species.
- Frequency = number of plots a given species was found.
- Relative frequency = number of plots containing a given species/total number of plots in which all species were sampled.
- Abundance = total number of trees.
- Relative abundance = Number of trees of a given species/number of trees of all species.
- Dominance = basal area per unit area; where by basal area was area of tree base calculated using radius at breast height (DBH/2).
- Relative dominance = dominance of a given species/dominance of all species put together.
- IVI = summation of relative density, relative frequency, and relative dominance.

Community-level analyses were based on ≈185 species encountered throughout the study, and correlation analyses for individual species were restricted to 65 "species" (64 species and one genus) with sample sizes of >30 trees. Species level analyses were conducted in two stages. First, I performed a principal component's analysis (PCA) to determine the extent of correlation among variables. The idea was to use these correlations as a basis for selecting variables to use in the next level of analysis, which correlated changes in individual species with distance from the edge. PCA summarizes parameters from a multidimensional space into a few components or axes. The PCA plot was based rotated data (Varimax rotation, Gamma = 1.0000). The varimax rotation is an orthogonal rotation that minimizes the number of variables with high loadings on each factor to simplify interpretation (Stenson and Wilkinson, 2002).

Analyses of correlations were based on fewer variables, selected to include all those with strongest loadings on principal components, but that differed widely from each other. This was to minimize needless duplication of results from use of closely correlated variables. The resulting factor loadings were used to select variables employed for correlation analysis. Selection aimed at determining variables that were as distinct from each other as possible, but also that had the highest loadings on principal components. These variables were log-transformed to improve linearity. As earlier analyses showed little overall influence of topography on edge-related distribution of plants in BINP (Olupot and Chapman, 2006; Olupot et al. in review), edge-related response (significant increase or decrease) is interpreted as "edge", rather than "topographic" influence. Estimate of percentage edge area was calculated using ArcView GIS, version 3.2a. All statistical analyses were performed in SYSTAT, Version 10.2.

To facilitate a comparison of responses by early succession (edge species) and late succession (typical forest species) species to the edge, species were classified as "edge", "forest", and "riparian" following Eggeling (1951) and Hamilton (1991). In the case of two *Macaranga* species which could not be categorized using the Ugandan data, they were assigned to the edge category following Davies et al. (1998).

## 3. Results

### 3.1. Analyses of edge effect at community-level

#### 3.1.1. Density
When analyzed using averaged values and a function plot derived from these values, tree density rapidly increased within the first 300 m, then slowly (Fig. 1a). A plot of standard errors based on values from individual plots showed that this was a property of the transects as well, and not just of the averaged values (Fig. 1b).

#### 3.1.2. Species richness
Pooled by distance category, species richness showed a rapid increase to 300 m, and then a gradual decline to 900 m (Fig. 2a). Analysis of data from individual plots showed that this was not true of individual transects (Fig. 2b). There was no peak, but a couple of spikes, with the spike at 500 m being particularly distinct. Species richness was generally similar for other samples, not excepting those along the boundary line.

#### 3.1.3. Species diversity
Patterns of species diversity were startling, given observed patterns in species richness. First, using pooled data, there was a trough, rather than a peak at 300 m, and then there were peaks at 100 and 500 m (Fig. 3a). Still, there was a general pattern of peaking between 100 and 700 m observed for species richness, and a gradual decline towards the interior. As for species richness, these patterns were not borne out by individual transects, for which there were three peaks (Fig. 3b).
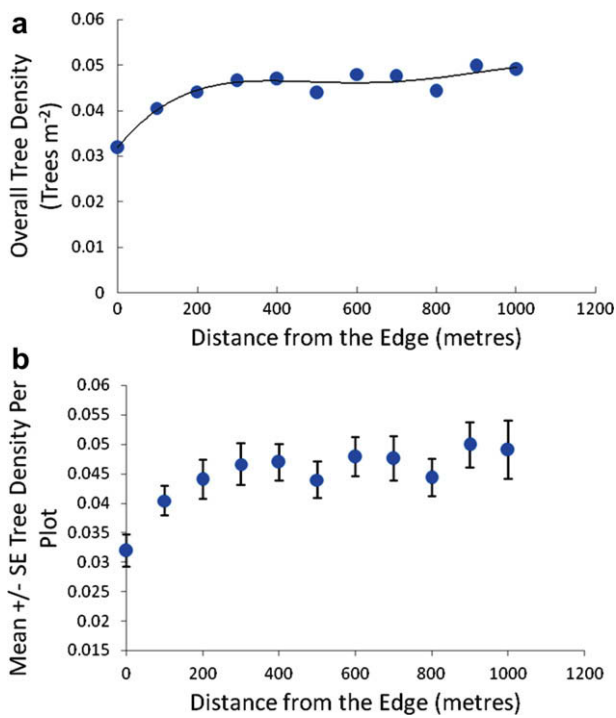
Fig. 1 – Variation in tree density (trees/m$^{-2}$) with distance from the forest edge: (a) pooled values approximated by a fourth order polynomial and (b) standard error charts based on data from individual sample plots.
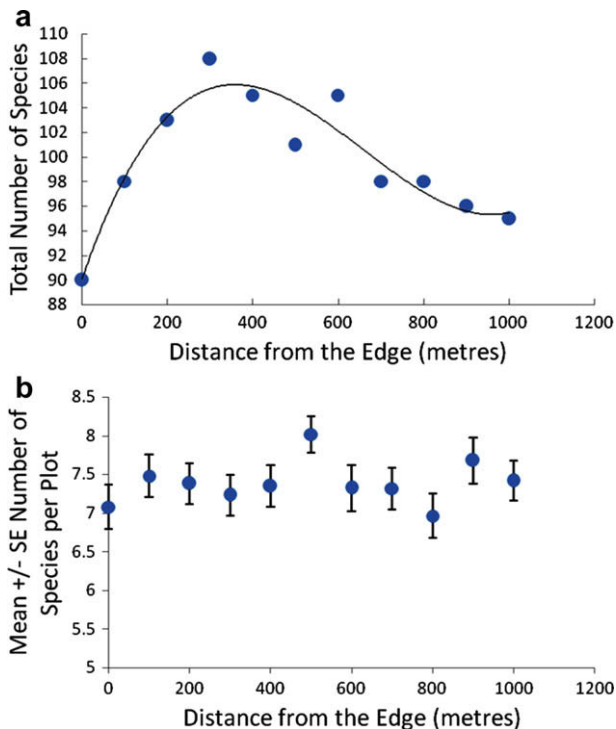


Fig. 2 – Changes in numbers of tree species with distance from the edge: (a) pooled data with trend approximated with a second order polynomial and (b) standard error charts of data from individual sample plots.
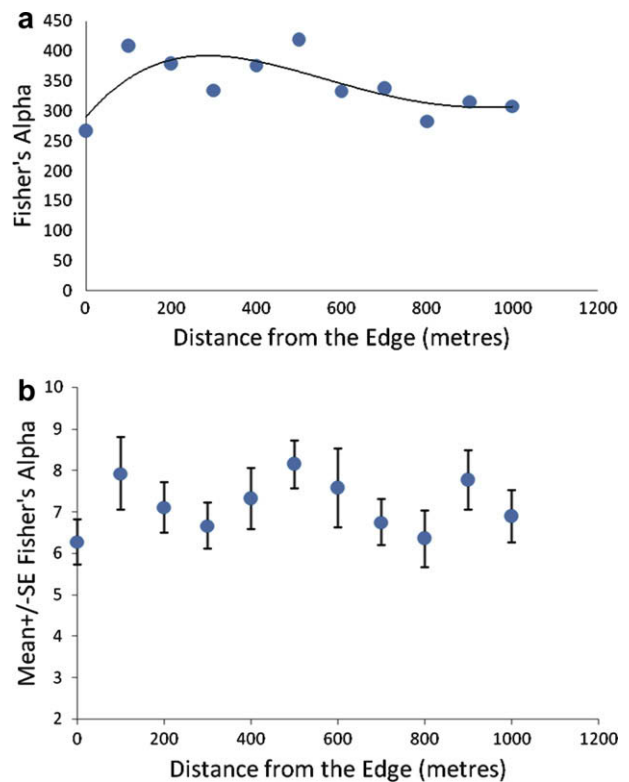


Fig. 3 – Changes in species diversity with distance from the edge: (a) using pooled data with the trend estimated with a second order polynomial and (b) standard error charts of data from individual sample plots.

#### 3.1.4. Measurements of stem girth (DBH)

Analyzed using averages for each distance category, measurements of stem girth (Fig. 4a) showed a vastly different pattern from that of species richness and diversity. Like density however, patterns from values averaged by distance categories were replicated by analyses of data from individual plots (Fig. 4b). Both types of analysis indicated a distinction between stem sizes at 0–400 m and 500–1000 m and that distinction was significant ($t$ test, $t = 2.105$; $p_{(two-tailed)} = 0.036$; $n = 649$). The consistency between patterns of pooled data and data from individual plots for both density and DBH suggests that both approaches were robust, though, they did not necessarily yield equivalent patterns of edge penetration. Edge penetration of 300–1000 m variously reported by analyses of DBH as well as density and species richness suggests that an area 13–38% of total park area of 321 km$^2$ is currently edge-influenced.

#### 3.1.5. Tree species composition

There was no detectable change in tree species composition along an edge-interior gradient (Fig. 5). Edge proximity was neither correlated with axis 1 ($r = −0.023$, $p = 1.000$, $n = 139$), nor with axis 2 ($r = 0.061$, $p = 1.000$; $n = 139$).

### 3.2. Analyses of edge effect at species level

PCA analysis used to explore the suitability of individual variables for analysis of species-specific responses showed heavy
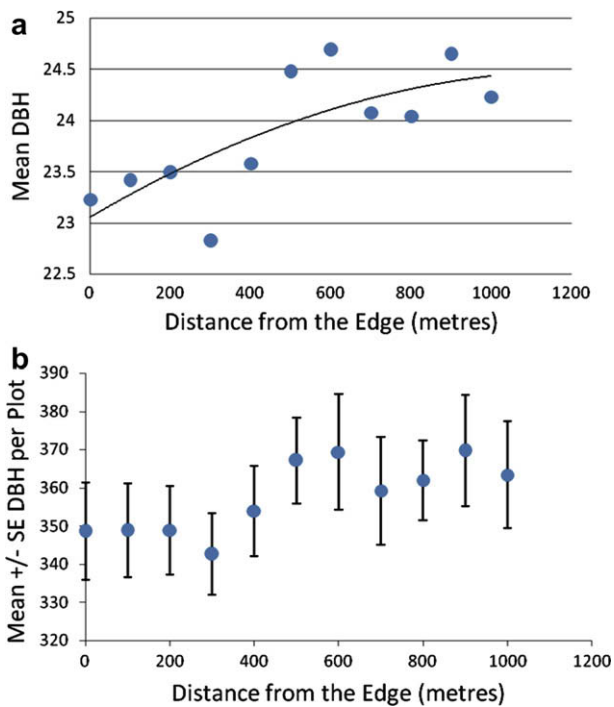
**Fig. 4 – Changes in mean tree size (diameter at breast height [cm]) as measured by diameter at breast height (DBH) with distance from the forest edge: (a) pooled data approximated by a second order polynomial and (b) standard error charts based on data from individual sample plots.**

loading on three components. Altogether, the loadings accounted for 95% of the variation in the matrix decomposed (Fig. 5). Factors (components) 1, 2, and 3 accounted for 61%, 20%, and 14% of the variance respectively (Table 1). DBH, density, relative abundance, relative frequency, relative dominance, basal area, and IVI were the most distinct in terms of the axes with which they were associated and extent of their loading on these axes (Fig. 6, Table 1). They were thus selected for correlation analysis (see Fig. 6).

There were significant correlations for 33 (51%) species (Table 2). Of these, 15 decreased, while 17 increased. Consistency of change direction occurred across variables where significant change was measured for all, but one species (*T. didymonstemon*) which decreased towards the interior when DBH was analyzed, but increased in terms of stem density.

Relative abundance and relative frequency measures showed the highest numbers of species responding to the edge (17 and 16, respectively). Both "edge" and "typical forest" species, by these analyses, responded to edge conditions (Table 2). Correlations with density showed significant correlations for 13 species, but 12 of those were "typical" forest species. Correlations using total basal area, IVI, relative dominance, and DBH showed significant relationships for 13, 12, 10, and 5 species, respectively.

The number of distinct species introduced by each analysis was highest (6) for density, followed by relative abundance and relative frequency (4 species each), DBH (3 species), total basal area (1 species). IVI and relative dominance did not, on their own reveal new species, but both of them introduced a
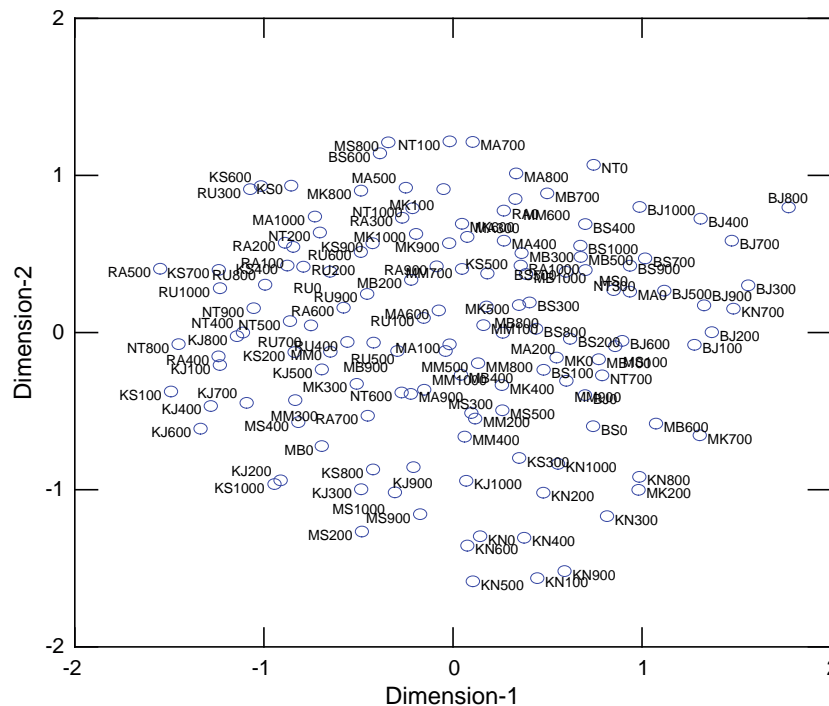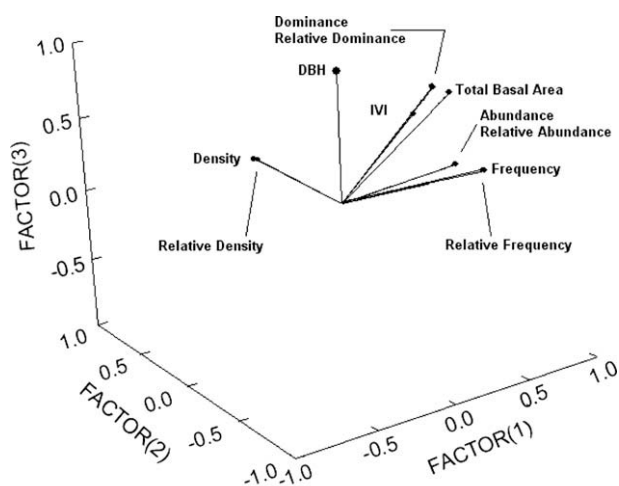


**Fig. 5 – NMDS plot showing similarities in species composition among plots. There was no tendency for plots to group according to distance from the edge, suggesting absence of edge-interior gradients in species composition. Plot identity: first two characters of each label are an abbreviation of the name of the parish while the following digits represent distance from the edge in metres.**

| Variable | Component | | |
| --- | --- | --- | --- |
| | 1 | 2 | 3 |
| DBH | −0.108 | −0.110 | <u>0.929</u> |
| Abundance | 0.953 | 0.182 | 0.000 |
| Relative abundance | <u>0.954</u> | 0.182 | 0.001 |
| Density | 0.082 | <u>0.988</u> | −0.014 |
| Relative density | 0.106 | 0.988 | −0.022 |
| Frequency | 0.971 | −0.044 | 0.019 |
| Relative frequency | <u>0.973</u> | −0.037 | 0.021 |
| Dominance | 0.740 | 0.165 | 0.605 |
| Relative dominance | <u>0.753</u> | 0.170 | 0.596 |
| Importance value index (IVI) | <u>0.832</u> | 0.430 | 0.325 |
| Total basal area | <u>0.758</u> | 0.038 | 0.592 |
| % of the total variance explained | 55.608 | 20.682 | 18.570 |

Table 1 – Rotated Loading Matrix (VARIMAX rotation, Gamma = 1.0000) from PCA analysis. Values of variables selected for correlation analyses are underlined.



**Fig. 6 – PCA Plot showing relationships among variables considered for assessment of edge-response by individual tree species. Relative measures were strongly related with the root congeners.**

new species (*S. guinense*) which decreased significantly away from the edge.

Patterns of change largely matched expectations based on classifications as edge or interior although not all "edge" and "forest" species decreased or increased significantly as would be expected. With exception of *M. cecropiodes* classified as an edge species which increased, only edge species decreased and only forest species increased towards the interior. Riparian species increased or decreased.

## 4.    Discussion and conclusions

Variables used to measure edge effects have rarely been analysed to assess their effectiveness in detecting edge effects. At least one study in the past noted potential difficulties of using the same variables despite the context: Laurance et al. (2006) in their analysis of effects of fragmentation on vegetation noted that had they used tree species richness alone, which parameter is commonly used in many island-biogeography

studies, they would have reached the erroneous conclusion that fragmentation and edges did not have any effect on tree communities.

Results from this study have shown that responses observed may vary depending on parameters selected and analyses used. At community level, analyses estimated the region influenced by the edge at 300–1000 m from the park boundary. Other analyses (like analysis of variation using inter-transect variation in richness and diversity; and analysis of species composition) showed no predictable edge-related variation. At species level, there were vast differences in response, varying from a strong effect to no effect, weak effect to a very strong effect, and in one case (for *T. didymonstemon*) showed a negative or positive effect depending on the parameter used. Such results can be a recipe for uncertainty about the depth of edge-influenced zones and effects of edges on forest plants.

The idea that an edge-influenced zone should be expected makes sense however, at least in theory. According to theory, generalist plants at home in any forest condition are likely to be more abundant at the edge than true forest species at home in the more mesic and stable interior microclimates. Given this, it becomes possible to anticipate a region of high species richness where generalists coexist with interior species (Laurance et al., 1998, 2006; Tabarelli et al., 1999).

Accordingly, estimating edge-width has usually been the undeclared interest of many studies of edge penetration but the results given here are one of the first for African forests. In forests around the world, edge-penetration has been estimated using both microclimatic and biological variables. Microclimatic effects (temperature, humidity, light intensity, and wind strength) have been reported to extend 100–150 m into the forest (Kremsater and Bunnell, 1999) in North American forests, and 15–60 m in central Amazonia (Kapos et al., 1997) and Australia (Turton and Freiburger, 1997). In North America, edge effect on forest organisms is thought to be concentrated within 50 m of edges, and within 400 m of roads (Kremsater and Bunnell, 1999). In Douglas-fir forests of Northwestern US, tree mortality and damage rates were detected to 300 m from forest edges (Chen et al., 1992), while in the Amazon within 60–100 m though elevated wind disturbance in these forests extended up to 500 m (Laurence et al.,

**Table 2 – Results of Pearson correlation analyses with distance from the edge, of tree species in Bwindi Impenetrable National Park, Uganda. Significant correlations (Bonferroni probabilities, p < 0.05) are represented. Correlations are based on log10-transformed values. Signs in the brackets show direction of change; with (+) indicating increase and (−) decrease towards the interior. The number of asterisks represents levels of significance, where * indicates significance at p = 0.05, ** at p = 0.01, *** at p = 0.001, and **** at p = 0.0001. Habitat assignments are taken from Eggeling (1951), but those marked & are taken from Hamilton (1991); and # taken from Davies et al. (1998).**

| Species | Habitat | DBH | Density | Relative abundance | Relative frequency | Relative dominance | IVI | Total basal area |
|---|---|---|---|---|---|---|---|---|
| Alangium chinense | Edge | | | | | | | |
| Albizia gummifera | Edge | | | (−)** | (−)** | (−)** | (−)*** | (−)** |
| Bridelia brideliifolia | Edge | | | (−)** | (−)* | (−)*** | (−)** | (−)** |
| Cassine aethiopica | Edge | | | | | | | |
| Croton macrostachys | Edge | | | (−)* | | | | |
| Galiniera coffeoides | Edge | | | | | | | |
| Harungana madagascariensis | Edge | | | (−)*** | (−)*** | (−)** | (−)** | (−)**** |
| Macaranga kilimandscharica | Edge | | | (−)*** | (−)**** | | (−)* | (−)** |
| Maesa lanceolata | Edge | | | (−)* | (−)* | (−)* | (−)* | (−)* |
| Maesopsis eminii | Edge | | | | | | | |
| Markhamia lutea | Edge | | | | | | | (−)* |
| Milletia dura | Edge | (−)* | | | | | | |
| Musanga cecropioides | Edge | | (+)** | (+)** | (+)* | (+)* | (+)** | |
| Nuxia congesta | Edge | | | | | | | |
| Polycias fulva | Edge | | | (−)* | (−)**** | (−)** | (−)*** | |
| Sapium ellipticum | Edge& | | (−)* | | | | | |
| Trema orientalis | Edge& | | | | | | | |
| Aidia micrantha | Forest | | | | | | | |
| Carapa grandiflora | Forest | | (+)* | | | | | |
| Casearia engleri | Forest | | | | | | | |
| Cassipourea spp. | Forest | | | | | | | |
| Celtis gomphylla | Forest | | | | | | | |
| Chryso albidum | Forest | | | | | | | |
| Dombeya goetzenii | Forest | | | | | | | |
| Drypetes gerrardii | Forest | | | | | | | |
| Drypetes sp. | Forest | | | (+)*** | (+)*** | | | |
| Drypetes ugandensis | Forest | | | (+)* | | | | |
| Entandro excelsum | Forest | | | | | | | |
| Funtumia africana | Forest | (+)* | | | | | | (+)** |
| Ilex mitis | Forest | | | | | | | |
| Leplaea mayombensis | Forest | | | | | | | |
| Myrianthus holstii | Forest | | (+)* | | | | | |
| Parinari excelsa | Forest | | (+)*** | (+)*** | (+)** | | (+)* | (+)* |
| Pittosporum manii | Forest | | (+)* | | | | | |
| Ritchiea albersii | Forest | | | | | | | |
| Strombosia scheffleri | Forest | | (+)* | (+)** | (+)*** | (+)** | (+)*** | (+)** |
| Tabernaemontana holstii | Forest | (−)** | | | | | | (−)** |
| Teclea nobilis | Forest | | | | | | | |
| Trilepisium phoberos | Forest | | (+)* | | | | | |
| Xymalos monospora | Forest | | (+)* | | | | | |
| Beilschmiedia ugandensis | Forest (Damp) | | | | | | | |
| Newtonia buchananii | Forest (Damp) | | | | | | | |
| Faurea saligna | Forest (montane) | | | | | | | |
| Ficalhoa laurifolia | Forest (montane) | | (−)** | | | | | |
| Agauria salicifolia | Forest& | | | | (−)** | | | |
| Allophylus macrobotrys | Forest& | | | | | | | |
| Anthocleista vogelli | Forest& | | | | | | | |
| Lepidotrichilia volkensii | Forest& | | | | | | | |
| Macaranga lanceolata | Forest& | | | | (+)* | | | |
| Musanga leo-errerae | Forest& | | (+)*** | (+)* | | (+)* | (+)*** | |
| Ocotea usambarensis | Forest& | | | | | | | |
| Rawnsonia lucida | Forest& | (+)** | (+)*** | (+)**** | (+)*** | (+)*** | (+)*** | (+)*** |
| Tetrorchidium didymonstemon | Forest& | (−)* | (+)* | | | | | |
| Trichilia rubescens | Forest& | | | | | | | |
| Prunus africana | Forest/Edge& | | (+)* | | | | | |
| Antiaris toxicaria | Forest/Savanna | | | | | | | |
| Ficus capensis | Forest/Savanna | | | (−)** | | | | |
| Dichaet corymbosa | Open forest& | | | | | | | |

| Species | Habitat | DBH | Density | Relative abundance | Relative frequency | Relative dominance | IVI | Total basal area |
|---|---|---|---|---|---|---|---|---|
| *Macaranga barteri* | Pioneer[#] | | | | (−)[**] | | | |
| *Macaranga sp.* | Pioneer[#] | | | | | | | |
| *Allanblackia kimbiliensis* | Riparian | | | | | | | |
| *Neoboutonia macrocarlyx* | Riparian | | | | (−)[*] | | | (−)[*] |
| *Psychotria mahonii* | Riparian | | | (+)[*] | (+)[*] | | | (+)[**] |
| *Symphonia globulifera* | Riparian | | | | | | | |
| *Syzigium guinense* | Riparian | | | | | (−)[*] | (−)[*] | |

Table 2 – *continued*

1997a,b). Also, foliage density in central Amazonia has been shown to increase up to 80–100 m from edges (Carmago and Kapos, 1995). The 300–1000 m estimate determined here therefore differs only slightly from the known range of edge penetration in forests around the world. However, this estimate would not have been possible had my sampling design been on a smaller scale as is usually the case (Ewers and Didham, 2008).

Compared to other forests for which edge-depth is widely believed to be determined by influence of microclimatic factors, edge-related patterns observed here probably have a direct anthropogenic origin. Observed influence of the edge in this forest is likely real, and not topographic as might be argued given the rugged terrain of the Bwindi landscape. That this is the case is illustrated by edge-related patterns of anthropogenic disturbance (e.g. timber harvesting, fires, collection of non-timber forest products, gold mining) reported by Thomas Butynski (Butynski, unpublished report, 1984), Howard (1991), and Olupot and Chapman (2006). More recently, Olupot et al. (in review) showed that the sheer impact of the edge, and not topography was a major determinant of edge-related distribution among 'useful' wild plants in the same forest. Correspondence among edge width estimates as determined by anthropogenic disturbance, tree density, and species richness, is further evidence of observed effects being largely anthropogenic. It is also interesting in that it suggests the possibility of different sampling protocols yielding the same result if reliable variables are used. The estimate based on anthropogenic influence was from counts of incidences of resource extraction in 50 m × 5 m plots placed end-to-end along transects; while these results are based on variable area plots 100 m apart along the same transects.

At species-level, analyses showed measures of abundance and distribution (relative abundance, relative frequency, and density) as generally better than tree girth (DBH) and species diversity; or those that integrated girth measurements with estimates of abundance (dominance, relative dominance, IVI). Density measurements are a measure of choice when predicting effect of disturbance on plants and this study indeed revealed the highest possible number of trees that were apparently negatively impacted by edge conditions. However, they did not show edge response by species known to thrive near edges. Measures of relative abundance and frequency showed response by both "edge" and "forest" species although the number of species shown to increase away from the edge was smaller than that revealed by density. In addition to density, inclusion of estimates of abundance and fre-

quency in simulations of forest change might be worth considering for new insights. These measures may also be useful indicators of forest change at the margins. From the results given here, it does not look like integrating measurements of girth or those partly dependent on girth would reveal dramatic insights of edge response in forest trees for conservation purposes.

Conservation action relies on well grounded data at species or community level. To reliably measure effect of reserve design, impact of human developments such as roads, influence of resource harvesting and fires, and extent of change in response to climate along edges for conservation purposes, it is important to select the right parameters. This study has shown that tree density, girth, and to some degree, species richness can be both sensitive and consistent in detecting extent of edge penetration; and that analyses of abundance, frequency and density may be good in detecting edge-response of individual species. More comparisons of variables and data from different sampling protocols and forest types should help reveal the best measures of edge penetration at community level and effect of edges on individual species.

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